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Reversing impact of phytoplankton phosphorus limitation on coastal hypoxia due to interacting changes in surface production and shoreward bottom oxygen influx

Liuqian Yu^{a,b}, Jianping Gan^{a,b,*}

^a Thrust of Earth, Ocean and Atmospheric Sciences, Department of Ocean Science, and Department of Mathematics, The Hong Kong University of Science and Technology ^b Southern Marine Science and Engineering Guangdong Laboratory (Zhuhai), China

ABSTRACT ARTICLE INFO Keywords: Phosphorus (P) limitation of phytoplankton growth is increasingly common in estuarine and coastal waters due Eutrophication to rising anthropogenic nitrogen input faster than that of phosphorus. However, the impact of P limitation on Coastal hypoxia coastal hypoxia remains inconclusive and is challenging to observe. By combining observations with results from Phosphorus limitation a three-dimensional physical-biogeochemical model off the Pearl River Estuary, we illustrate that during the Physical-biogeochemical model summer upwelling period, the impact of P limitation reverses from suppressing hypoxia to amplifying hypoxia as P-limitation severity decreases. When P limitation is severe in the ecosystem (i.e., P limitation extensively covers the stratified waters where hypoxia tends to develop), the surface primary production and the coupled bottom oxygen consumption are diluted along the upstream-downstream axis because of the P limitation. In addition, the increased downstream bottom oxygen level enhances the shoreward bottom oxygen influx. These effects, together, reduce coastal hypoxia. In contrast, when P-limitation severity is low (i.e., P limitation is spatially constrained), the downstream relocated surface production reduces upstream hypoxia but increases downstream hypoxia, which subsequently weakens the shoreward bottom oxygen influx and hence lowers its capacity to relieve upstream hypoxia. The net effect can amplify the coastal hypoxic extent. Our results emphasize how different P-limitation severity can reverse its impact on coastal hypoxia due to the interacting changes in surface production and bottom oxygen influx. We propose the potential of using the spatial extent of P limitation as a

proxy to predict its impact on coastal hypoxia and support ecosystem nutrient management.

1. Introduction

Nitrogen (N) and phosphorus (P) availability limit phytoplankton production in most aquatic ecosystems. Such nutrient limitation, however, is overcome when there is excessive anthropogenic N and P introduced to the ecosystems. An excessive nutrient supply stimulates phytoplankton growth, increases decomposition of phytoplankton organic matter, and triggers bottom water hypoxia (dissolved oxygen < 2 mg/L). The hypoxia caused by nutrient over-enrichment occurs globally in estuarine and coastal waters, and its frequency, extent, and duration are projected to increase as the anthropogenic nutrient delivery continuously rises (Breitburg et al., 2018). In addition to the increasing nutrient loads, the N/P proportion of the nutrient runoff to coastal ecosystems has substantially increased and exceeds the average stoichiometric need for phytoplankton growth (i.e., the canonical Redfield

ratio of 16:1) (Glibert et al., 2014; Wang et al., 2021). The elevated N/P proportion is primarily due to the increased anthropogenic use of N relative to P at a global scale (Glibert et al., 2013) and the higher mobility and more diffuse sources of N than P (Peñuelas et al., 2012).

Driven by the faster increase in river-delivered dissolved inorganic N (DIN) relative to dissolved inorganic P (DIP), temporary P limitation has become more common in estuarine and coastal systems (Conley 1999; Paerl, 2009; Quigg et al., 2011; Wang et al., 2021; Xu et al., 2008; Yin et al., 2004). Generally, P limitation is recognized to reduce the capacity of upstream water to assimilate DIN, thereby enhancing DIN transport downstream to fuel primary production in more saline N-limited waters (Paerl et al., 2004). However, the impact of P limitation on coastal hypoxia is challenging to observe because monitoring the effect on entire coastal systems at sufficient resolution and scale is difficult and manipulating N and P inputs to conduct whole-ecosystem experiments is

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^{*} Corresponding author at: Department of Mathematics, The Hong Kong University of Science and Technology, Kowloon, Hong Kong. *E-mail address:* magan@ust.hk (J. Gan).

not feasible (Laurent and Fennel, 2017). As a result, whether P limitation worsens or alleviates hypoxia remains inconclusive (Fennel and Testa, 2019; Laurent and Fennel, 2014; Scavia and Donnelly, 2007) and is hypothesized to be affected by a system's geometry (Laurent and Fennel, 2017). For example, P limitation is more likely to amplify hypoxia in a one-dimensional through-flow system, where a downstream shift of production and the accompanying oxygen sink would cause the hypoxia to relocate downstream. On the contrary, P limitation might suppress hypoxia in a dispersive open system, where the stratification weakens downstream such that the downstream enhanced oxygen sink would not trigger downstream hypoxia (Laurent and Fennel, 2014).

In this paper, we hypothesize that the impact of P limitation reverses from suppressing coastal hypoxia to amplifying hypoxia when P-limitation severity decreases. The reversal occurs independent of a system's hydrodynamic conditions but is purely driven by the limitation-induced interacting changes in surface primary production and the shoreward bottom oxygen influx. The bottom oxygen influx is associated with the bottom water intrusion, a characteristic feature in estuarine circulation and coastal upwelling systems. P limitation affects the spatial distribution of surface phytoplankton production and thus the deposition flux of organic matter reaching the bottom waters or sediments and the subsequent remineralization-induced oxygen consumption. The altered oxygen consumption influences the bottom oxygen level and the horizontal oxygen gradient, consequently altering the shoreward bottom oxygen influx despite that the velocity of bottom intrusion current is not modified.

Our hypothesis is illustrated in Fig. 1. During severe P limitation (e. g., when there are large river inputs of DIN and DIP with a high N/P ratio) (Fig. 1A, B), the P limitation extensively covers the stratified water where hypoxia tends to develop. As a result, the surface phytoplankton biomass and its coupled bottom oxygen consumption are diluted along the upstream-downstream axis due to the P limitation. In addition, the elevated downstream bottom oxygen level enhances the shoreward

bottom oxygen influx. These effects jointly mitigate hypoxia. In contrast, when P-limitation severity is lower (e.g., when there are moderate river inputs of DIN and DIP despite a high N/P ratio) (Fig. 1C, D), the water rapidly transitions from being P-limited to being N-limited along the upstream-downstream axis. The dilution of the surface primary production reduces the upstream bottom oxygen sink but enhances the bottom oxygen sink in the N-limited downstream water. This enhanced downstream oxygen sink may turn the downstream bottom oxygen level (whether hypoxic or not) further reduces the shoreward bottom oxygen influx and hence its capacity to replenish upstream hypoxia. As a result, the net effect of P limitation on the overall hypoxic extent can be amplification.

This study aims to verify the hypothesis described in the previous paragraph, namely, how and why the impact of P limitation on coastal hypoxia reverses depending on P-limitation severity. To that end, we carry out a series of nutrient scenario simulations in the Pearl River Estuary (PRE) in the northern South China Sea using a validated threedimensional (3D) physical-biogeochemical model. We examine the summer oxygen dynamics and hypoxia in PRE during times of upwelling and investigate how and why they change under different nutrient limitation conditions. The results confirm our hypothesis that the impact of P limitation on coastal hypoxia reverses due to the interacting changes in surface production and the shoreward bottom oxygen influx under different levels of P-limitation severity. We also propose that the spatial extent of P limitation, which can reflect the severity of the limitation and is detectable by measuring nutrient concentrations, can be used as a proxy to predict the unobservable impact of P limitation on coastal hypoxia.



Fig. 1. Schematic showing how P limitation affects the hypoxic extent and associated ecosystem processes in scenarios of (**A**, **B**) high P-limitation severity and (**C**, **D**) lower P-limitation severity during summer when strong water column stratification exists. Both scenarios have inorganic nitrogen (N) to phosphorus (P) ratio of the river nutrient input exceeding the Redfield ratio of 16. Note the size of arrows representing river N and P inputs are not to scale. For both scenarios, the top panels represent the N-only case, where only one nutrient element, N, is considered to affect the primary production (i.e., assuming no effect from P), and the bottom panels represent the Control case where N and P co-regulate primary production. The differences between Control and N-only cases represent the effect of P limitation on the ecosystem processes. In panels (B) and (D), the "enhanced" or "reduced" influx and consumption in Control case are relative to those in N-only case, indicating the effect of P limitation.

2. Material and methods

2.1. Study region

The PRE in the northern South China Sea (Fig. 2A) receives excessive amounts of anthropogenic nutrients from the Pearl River, the second-largest river in China in terms of freshwater discharge (3.26×10^{11} m³ yr⁻¹) (Zhao, 1990). Just as in the rest of the world, over the past few decades, the Pearl River has experienced an increase in river N and P loads that have a remarkably high DIN/DIP ratio (>100). As a result, the surface DIN concentration and DIN/DIP ratio in the PRE has significantly increased. The increase is reflected in monthly DIN and DIP data

Pearl River

discharge

23

22.5

22

21.5

21

112.5

Α

Latitude

from 1991 to 2020 sampled at a station in the upper PRE (Fig. 3A, B). The time-series data is collected and analysed by the Hong Kong Environmental Protection Department (EPD; www.epd.gov.hk). In addition to the river input, the submarine groundwater delivers nutrients at a high N/P ratio to the estuarine and coastal waters (Dai et al., 2021; Liu et al., 2018), which may exacerbate the P limitation. The contribution of submarine groundwater is not considered in this study as we focus on the impact of P limitation at a large spatial scale of coastal waters where Pearl River input is the dominant nutrient source.

In addition to the impact of the large river discharge, the circulation off the PRE is profoundly affected by the wind-driven coastal current. Notably, during the wet season (April to September), when nearly 80%



Time series

station

Hona Ko

3 5

113.5

Bathymetry (m)

20

>50

115.5

10

114.5



Fig. 3. Time series of the observed surface (A) dissolved inorganic nitrogen (DIN) concentration and (B) ratio of DIN to dissolved inorganic phosphorus (DIP) at the monthly monitoring station marked in Fig. 2A. The red line indicates the linear regression (in the form of y=ax) with a significant correlation coefficient (r) at p<0.05.

of the annual Pearl River discharge occurs, the southwesterly monsoon wind prevails that favours producing upwelling. The strong seaward surface flow, rich with nutrients, converges with the wind-driven alongshelf current in the coastal transition zone (CTZ) off the PRE. This convergence creates a stable water column that restricts the vertical oxygen supply and favours the accumulation of phytoplankton-derived organic matter (OM) and river-delivered terrestrial OM, all of which promote hypoxia formation in the CTZ (Li et al., 2020; Yu et al., 2020).

2.2. Model description

We conducted a process-oriented investigation using a coupled physical-biogeochemical model (Fig. 2). Details of the model setup, parameterization, and validation are presented in previous studies (Li et al., 2020; Liu and Gan, 2020; Yu et al., 2020; Yu and Gan, 2021). Briefly, the physical component of the model is a 3D high-resolution configuration of the Regional Ocean Modelling System (ROMS) (Shchepetkin and McWilliams, 2005) for the PRE and its adjacent shelf in the northern South China Sea (Fig. 2A). The model adopts an adaptive horizontal resolution, gradually decreasing from ultrahigh (\sim 0.1 km) in the estuary and inner shelf to \sim 1 km over the shelf at the southern open boundary. In addition, it has 30 terrain-following vertical layers with refined resolution (<0.2 m) near the surface and bottom.

The biogeochemical component (Fig. 2B, C) is adapted from the Nbased model developed by Fennel et al. (2006) and includes cycling of oxygen (Fennel et al., 2013), phosphorus (Gan et al., 2014; Laurent et al., 2012), and terrestrial organic matter (Yu et al., 2015, 2020). Following Laurent et al. (2012), the model adopts the minimum functional form to estimate nutrient limitation, assuming that phytoplankton growth depends on the most limited nutrient (N or P). Specifically, we calculate the DIN limitation factor using the formula, $L_N = \frac{N03}{k_{NO3}+NO3} \times \frac{1}{1+NH4/k_{NH4}} + \frac{NH4}{k_{NH4}+NH4}$, and the DIP limitation factor with the formula, L_P $=\frac{DIP}{k_{DIP}+DIP}$, where k_{NO3} , k_{NH4} , and k_{DIP} are the half-saturation constants for phytoplankton uptake of nitrate (NO₃), ammonium (NH₄), and DIP. The L_N and L_P range from 0 to 1, with the smaller value indicating stronger limitation. We then compute the nutrient co-limitation factor as $L = \min(L_N, L_P)$, and apply it to the formula for the specific phytoplankton growth rate (μ) as $\mu = \mu_{max}(E,T) \times L$, where $\mu_{max}(E,T)$ is the light- and temperature-dependent maximum growth rate of the phytoplankton. We here define *L* above 0.75 as weak or absence of nutrient limitation, and *L* decreasing from 0.75 to 0 as moderate to strong limitation.

The oxygen dynamics are governed by air-sea exchange, physical transport, and biogeochemical oxygen production and consumption processes (Fig. 2C). The equation for the evolution of oxygen (O_2) can be written as:

$$\frac{\partial O_2}{\partial t} = -\mathbf{u} \cdot \nabla O_2 + \nabla \cdot (\kappa \nabla O_2) + PP + WCR + F_{bf}$$

where the five terms on the right-hand side represent advection, diffusion, photosynthetic production (*PP*), water column oxygen consumption (*WCR*), and boundary oxygen fluxes, respectively. Here **u** is the velocity vector and κ is the eddy diffusivity. The term *WCR* represents the sum of water column consumption processes, including zooplankton respiration, nitrification, and remineralization of organic matter. The term F_{bf} represents the boundary oxygen fluxes and is only applied to the surface layer as the air-sea oxygen exchange and the bottom layer as the sediment oxygen consumption. F_{bf} is 0 at the layers between the surface and bottom. Parameterizations of the oxygen terms are detailed in Yu et al. (2020) and Yu and Gan (2021).

The coupled physical-biogeochemical model is driven by simplified but representative summer forcings to conduct process-oriented investigations. The process-oriented approach is better suited to distinguish the processes at work under the complex multi-forcing processes and has been proven useful for investigating the dynamic physical and biogeochemical interactions in the study region (Gan et al., 2014; Li et al., 2020; Yu et al., 2020). Briefly, the model is forced with a steady and spatially uniform southwesterly (upwelling-favourable) wind that characterizes the typical summer southwesterly monsoon wind. Solar radiation with a diurnal cycle is applied following Gan et al. (2014). River discharge rate, temperature, salinity, and concentrations of nutrients, oxygen, and organic matter are based on the long-term summer monitoring data and historical measurements (Cai et al., 2004; Ni et al., 2008). Horizontally uniform initial conditions generated from observational profiles are used to initialize the model and investigate the spatiotemporally evolving processes following Gan et al. (2014). An open boundary condition that concurrently accommodates tidal and subtidal forcing is applied at the open boundaries (Liu and Gan, 2016) in which external subtidal flows are provided by an idealized cross-shelf two-dimensional model simulation following Gan and Allen (2005) and major tidal constituents (M2, S2, K2, N2, K1, O1, Q1, P1, and M4) are obtained from the Oregon State University Tidal Inversion Software (OTIS) (Egbert and Erofeeva, 2002). Lastly, a passive radiation condition is adopted for the biological variables at all three open boundaries.

2.3. Field observations and model validation

Nutrient observations at the surface and bottom waters (locations shown in Fig. 2A) are used to examine the nutrient limitation conditions and validate the model results. The field observations are from cruise surveys during the summers of 2015 and 2017 when coastal upwelling prevailed. Sampling and analysis methods are presented in Lu et al. (2018) and Li et al. (2020). The DIN concentration was computed as the sum of observed NO₃, NO₂, and NH₄ concentrations. For some sampling stations where NH₄ and/or NO₂ observations were not available, DIN was computed as NO₃+NO₂ or NO₃. Given the generally higher NO₃ concentration than the NH₄ and /or NO₂ in part of the sampling

stations will have little impact on the presented distribution pattern of the DIN.

Previous model validation by field observations showed that the coupled model realistically captures the characteristic circulation and ecosystem features in and off the PRE during summer (Liu et al., 2020; Liu and Gan, 2020; Li et al., 2020, 2021; Yu et al., 2020). These features include the distinct two-layer estuarine circulation (surface freshwater outflow and bottom seawater inflow) within the estuary (Fig. 4C, D), seaward extended nutrient-rich river plume (Fig. 4A), wind-driven coastal upwelling (Fig. 4B), and hypoxia development in the CTZ off the PRE (Fig. 4B). Also noticeable is that the shelf water downstream of the CTZ has relatively higher bottom water oxygen (Fig. 4B), thereby enabling the shoreward bottom oxygen influx to become a source of oxygen to replenish the oxygen-deficient CTZ during prevailing summer upwelling (Fig. 4B, C).

Here we further show that the model reasonably reproduces the observed DIN and DIP concentrations (Figs. S1, S2 in the Supplement) and captures the observed spatial pattern of nutrient limitation (Fig. 5). Both the observations and the simulation show that the limitation primarily shifts from weak P limitation (limitation factor L>0.75) within the estuary and the adjacent CTZ to strong P limitation (L<0.3) downstream of the plume-affected waters and shifts to N limitation in the saline coastal marine waters (Fig. 5).

2.4. Model experiments

To quantify the impact of the P limitation, we performed two types of simulations: **Control** simulations, which used the multi-nutrient model with N and P cycling shown in Fig. 2B, and **N-only** simulations, which had a setup identical to the control simulations except that we disabled the P cycling in the multi-nutrient model to enable N as the only limiting nutrient. We used the difference between the Control and N-only simulations, computed as Control minus N-only, to represent the impact of the P limitation on the ecosystem.

We first conducted a pair of simulations with standard river nutrient concentrations (NO₃, NH₄, and DIP at 120, 3, and 0.8 mmol/m³, respectively) that we called the Baseline simulations. The Baseline simulations represent the 'Severe P limitation' scenarios as demonstrated by the extensive P limitation shown in Fig. 5B. Next, to create scenarios with 'lower P-limitation severity', we conducted three pairs of simulations whose setups were identical to the Baseline pair except we simultaneously reduced the river DIN and DIP concentrations by 60%, 70%, and 80%, respectively (called the '-x%N&P' scenarios where *x* denotes the percentage reduction).

To further examine the sensitivity of the results to the variable freshwater river discharge, we carried out scenarios of different P-limitation severity under different riverine inputs of freshwater while preserving the nutrient loading (i.e., by adjusting the riverine nutrient concentrations). Specifically, the first group of four pairs of simulations adopted the Baseline freshwater discharge (18,400 m^3 /s), while the



Fig. 4. Model-simulated (by Control simulation) circulation and ecosystem features in and off the Pearl River Estuary during summer under the influence of upwelling-favourable wind. **(A)** Spatial distribution of simulated surface dissolved inorganic nitrogen (DIN) with surface velocity (red arrows) superimposed onto the map. The solid red lines depict the boundaries of the coastal transition zone (CTZ), and the curvy magenta lines denote contours of surface salinities at 24 and 33. The gray contours mark the bathymetric depths of 5, 10, 20, 30, 40, and 50 m, with the thicker gray representing the 20 m contour line. The red circles indicate the locations of seven river outlets. **(B)** Same as (A) but for bottom dissolved oxygen (color map) and bottom velocity (red arrows). **(C)** Distribution of simulated dissolved oxygen (DO) along a seaward transect, with red and magenta arrows depicting the seaward and shoreward velocities, respectively, and gray contours marking the salinity. The location of the seaward transect is denoted by the red line crossing the CTZ in panel (B). **(D)** Distribution of simulated velocity across the west-east transect (i.e., the southern boundary of the CTZ). The magenta line marks the velocity at 0 and gray contours mark the salinity. Here positive values (in red) denote shoreward velocity while negative values (in blue) denote seaward velocity.



Fig. 5. (A) Observed (from field surveys) and (B) model-simulated (by Control simulation) nutrient limitation factor L (0 < L < 1) at surface waters. Blue and red colours represent N and P limitation, respectively, and light to dark color indicates increasing degree of limitation. In each panel, the gray contours mark the bathymetric depths of 5, 10, 20, 30, 40, and 50 m, with the thicker gray representing the 20 m contour line. In panel (B), the solid red lines depict the boundaries of the coastal transition zone, the curvy purple lines denote contours of surface salinities at 24 and 33, and the thin red and blue contours indicate P limitation factor at 0.75 and N limitation factor at 0.75, respectively.

other groups had freshwater discharge reduced by 20% and 50%, respectively (referred to as -20%FW and -50%FW). The three discharge values we adopted are within the variable range of summer discharge of the Pearl River. We ran each model simulation for 45 days, during which the simulated biogeochemical fields reached quasi-steady states after about 30 days. We based our analyses on model outputs averaged over a complete neap-spring tidal cycle (i.e., Day 38 to 45).

3. Reversing impact of P limitation on coastal hypoxia

3.1. Impact under severe P limitation

We investigate the impact of severe P limitation on coastal hypoxia and related oxygen processes by first examining the Baseline simulations. Fig. 6A presents the changes caused by P limitation in the watercolumn integrated primary production. The changes in production show three spatial regimes: a slight reduction in the upper estuary and in the majority of the CTZ where the P limitation is relatively weak; a substantial decrease in the intermediate region of the plume where P is severely limited; and a slight increase farther downstream of the plume (Fig. 6A). A weakened production is expected to reduce the subsurface oxygen consumption and thereby increase bottom water oxygen concentration, and vice versa. Yet, interestingly, a sizable spatial misalignment exists between the limitation-induced changes in the primary production (Fig. 6A) and the bottom oxygen (Fig. 6B). Generally, a marked increase in bottom oxygen occurs in the majority of the CTZ and is located more shoreward than the substantial reduction in production. This misalignment is also confirmed by the weak correlation between the changes in production (correlation coefficient r=-0.28) or the bottom oxygen consumption (r=-0.47) with the changes in bottom oxygen level (Fig. S3).

The enhanced bottom oxygen level in the CTZ (the hypoxia hotspot) due to the P limitation remarkably reduces the hypoxic extent (60% reduction in area and 79% in volume) and retracts the hypoxia towards the shallower waters. The latter is further depicted by that the bathymetry in which the 90th percentile of the hypoxia falls is shallower in the Control simulation (18.5 m) than in the N-only simulation (25 m) (Fig. 7A). Additionally, Fig. 7B shows that hypoxia mainly occurs in waters shallower than where most of the remarkable decrease in production occurs, consistent with the spatial decoupling of elevated bottom oxygen and weakened production shown in Fig. 6A, B. It follows that the *in situ* or local changes in biogeochemical oxygen rates can only partially explain the enhanced bottom oxygen level and reduced hypoxia in the CTZ. The lateral transport of subsurface oxygen, an external source of oxygen, must play a non-negligible role. Indeed, while P limitation reduces the upper water oxygen level by suppressing the surface production, it increases the subsurface oxygen level due to the reduced subsurface oxygen sink (Fig. 6C). The altered oxygen levels lead to a decrease in upper water oxygen outflux and an increase in the subsurface oxygen influx to the CTZ (Fig. 6D). The enhanced subsurface oxygen influx subsequently replenishes the oxygen-deficient bottom water in CTZ and contributes to reducing hypoxia.

To further quantify the relative importance of the changes caused by P limitation in the external oxygen flux and the local (internal) oxygen processes on the changes in oxygen levels, we computed the oxygen budget near the bottom of the CTZ (Fig. 7C). For the bottom water in CTZ, horizontal advection and vertical mixing act as oxygen sources, whereas the net biogeochemical process (primary production minus water column and sediment oxygen consumption) is an oxygen sink. The effect of P limitation enhances the horizontal advection of oxygen by 21% but reduces the vertical mixing of oxygen by 18% and the net biogeochemical sink by 12%. The enhanced horizontal advection of oxygen due to the strengthened shoreward oxygen influx is considered a change in external oxygen source caused by the P limitation. On the contrary, both the weakened vertical mixing of oxygen (due to a weakened vertical oxygen gradient) and the reduced net biogeochemical oxygen sink are attributed to the P-limitation-suppressed surface production and hence considered to be the changes in local (internal) oxvgen processes. The changes in vertical mixing and net biogeochemical oxygen sink add up to a local net oxygen sink. This local net oxygen sink increases by 20% due to the P limitation, a magnitude comparable to the 21% increase in horizontal oxygen advection.

In summary, P limitation increases the local (internal) net oxygen sink and the external oxygen source, with the former amplifying hypoxia and the latter mitigating hypoxia. The changes in the two interacting processes are equivalent in magnitude but work oppositely to determine the net effect of P limitation on the bottom water oxygen level and hypoxia. This net effect significantly reduces hypoxia off PRE under the severe P limitation.

3.2. Impact under lower P-limitation severity

Section 3.1 reveals that severe P limitation markedly reduces hypoxia due to the combined effects of downstream-diluted primary production and enhanced shoreward subsurface oxygen influx. Here we investigate how the conclusion might change under lower P-limitation severity by comparing scenarios with the same physics but less severe P limitation conditions. Then we examine whether the changes hold for other river freshwater inputs.

First, we examine the different limitation severity scenarios using the Baseline freshwater discharge. As the P-limitation severity weakens (indicated by the shrinking percentage of P-limitation area in Fig. 8A



Fig. 6. Effect of P limitation (quantified as Control minus N-only) on primary production, oxygen distribution, and oxygen transport. **(A, B)** Same as Fig. 4A but for the limitation-induced changes in (A) water column integrated primary production and (B) bottom dissolved oxygen (DO). **(C)** Limitation-induced change in the vertical distribution of DO along the west-east alongshore transect (shown in Panel B). The gray lines denote DO change at 0. **(D)** Vertical profiles of the horizontally integrated oxygen transport across the west-east transect for the Control (blue) and N-only (red) simulations, with negative values indicating seaward outflow and positive values indicating shoreward inflow. The shaded area denotes the temporal variation during the neap-spring tidal cycle (Day 38–45).

and Fig. S4), the effect of P limitation on suppressing the production and increasing bottom water oxygen weakens and consequently reverses so that production increases and downstream (surface salinity >24) bottom water oxygen decreases (Fig. S4). The impact of the reversal is reflected in the altered vertical oxygen distribution in the downstream alongshore transect. The vertical distribution shows that the limitation reduces upper water oxygen and increases the subsurface oxygen level when P limitation is severe (Fig. 9A), but this pattern weakens and eventually reverses to increase upper water oxygen and reduce subsurface oxygen when P-limitation severity decreases (Fig. 9B-D; the reversal occurs in -70%N&P and -80%N&P). Directly affected by the change in limitation-altered subsurface oxygen level, the shoreward subsurface oxygen inflow changes from increasing to decreasing as P-limitation severity decreases (Fig. 8B). It subsequently affects the impact of P limitation on horizontal oxygen advection within the CTZ, which reverses from enhancing to weakening its capacity to replenish the oxygen-deficient zone (Fig. 8C). A similar reversing trend appears in the limitation-altered local net oxygen sink (Fig. 8D).

The declining and reversing trend of the effect of P limitation on oxygen concentration and regulating processes leads to a declining and reversing impact on the hypoxic extent (Fig. 8E-F). Specifically, the limitation-induced reduction in downstream hypoxia declines as P limitation becomes less severe (e.g., reduction in downstream hypoxic volume decreases from 84% in the Baseline scenario to 10% in -60% N&P) and ultimately shifts to increase hypoxia under very low P-limitation severity (e.g., downstream hypoxic volume increases by 5% in -70%N&P and 11% in -80%N&P) (Fig. 8E). The above trend holds for the hypoxic volume in the entire system except that the hypoxia increase

has not happened yet, even in the scenario of lowest (most spatially constrained) P-limitation severity under this Baseline freshwater input (Fig. 8F).

The reversing impact from high to lower P-limitation severity generally holds for different hydrodynamic conditions created by varying river discharge inputs (Figs. 8, 9), demonstrating the robustness of our results. The noticeable difference is that the P-limitation area shrinks when the river freshwater discharge is reduced despite preserving river nutrient loads (Fig. 8A). The shrinkage occurs because the reduced discharge reduces the plume's extent and leads to more upstream concentrated N and P for biological recycling. As a result, under the lower freshwater discharge, the declining P-limitation impact steepens to reach the reversing point earlier (Fig. 8B-D). Also, the P-limitation impact shifts to slightly expanding the hypoxia for scenarios of lowest P-limitation severity (-70%N&P and -80%N&P) in the -50% FW scenario (Fig. 8F).

4. Discussion

Temporary P limitation of phytoplankton growth is more commonly observed in estuarine and coastal hypoxic systems (Fennel and Testa, 2019) due to rising anthropogenic nutrient contributions that elevate the N/P ratio (Glibert et al., 2013). However, despite the potential importance of P limitation to hypoxia development, observations of P-limitation impact on coastal hypoxia are scarce primarily due to the difficulty in observing the effect. Quantitative assessment of P-limitation impact on hypoxia thus largely relies on numerical modeling but such assessment is currently limited to few hypoxic systems (Laurent and

source

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Fig. 7. Effect of P limitation (comparing Control and N-only simulations) on oxygen-related processes and hypoxia. **(A)** Limitation-induced change (quantified as Control minus N-only) in water column integrated primary production (PP) as a function of bathymetry, where the red dots highlight the hypoxic locations, and the dashed vertical line marks the 25 m bathymetry location. **(B)** Histogram distribution of hypoxia along the bathymetry for the Control and N-only simulations, where the dashed colored lines indicate the respective bathymetry values in which the 90th percentile hypoxia falls. **(C)** Bar graph comparing the Control simulation with the N-only simulation for the oxygen budgets of the near-bottom water in the coastal transition zone. Hadv denotes the horizontal advection; vmix denotes the vertical mixing; NetBGCsink is the net biogeochemical oxygen sink (i.e., the sum of primary production, water column oxygen consumption, and sediment oxygen consumption); and NetLocal is the net local oxygen sink (i.e., the sum of Vmix and NetBGCsink). The values on top of the bars denote the limitation-induced percentage change for each oxygen term.

Fennel, 2014, 2017; Fennel and Laurent, 2018). As a result, it remains unsettled why P limitation is considered to aggravate hypoxia in some systems (Conley 1999; Paerl et al., 2004) but mitigate hypoxia in others (Laurent and Fennel, 2014). Laurent and Fennel (2017) proposed that the effect of P-limitation may be related to a specific system's geometry, where P limitation is more likely to amplify hypoxia in one-dimensional flow-through systems (e.g., Neuse River Estuary) but tend to alleviate hypoxia in open dispersive systems (e.g., northern Gulf of Mexico affected by Mississippi River plume). While the proposal helps explain the contrasting effects of P-limitation on hypoxia among different systems, question remains at whether and why the effect can contrast in the same hypoxic system (e.g., Scavia and Donnelly 2007; Laurent and Fennel 2014).

Combining observations and results from a coupled physicalbiogeochemical model off a large eutrophic estuary during summer upwelling conditions, we validate the hypothesis that the impact of P limitation reverses from suppressing coastal hypoxia to amplifying hypoxia when P-limitation severity decreases (Fig. 1). We show that the reversal is independent of a system's hydrodynamic conditions. It is driven by the interacting limitation-induced changes in the surface primary production and the shoreward bottom oxygen influx. When P limitation is severe (or spatially extensive), the downstream-diluted primary production reduces the bottom oxygen sink in most of the plume-impacted waters and enhances the shoreward bottom oxygen influx because of the increased downstream oxygen level. These effects jointly reduce hypoxia in the entire coastal system. When P-limitation severity is lower (or spatially constrained), while the diluted production mitigates upstream hypoxia by lowering the bottom oxygen sink, the primary production relocates downstream and increases oxygen consumption and hence hypoxia downstream. The reduced bottom oxygen downstream subsequently reduces the shoreward oxygen influx that could otherwise alleviate upstream bottom hypoxia. As a result, the net effect of lower P-limitation severity amplifies hypoxia in the ecosystem.

The reversing impact of P limitation on coastal hypoxia has important management implications for PRE and other hypoxic systems. The PRE is an outstanding example of a large eutrophic estuary. Under the present excessively high river DIN and DIP loads with a high N/P ratio (>100), P is the dominant limiting nutrient in most of the water affected by the river plume off the PRE during summer. However, although a high N/P ratio prevails in the inner estuary and the neighboring CTZ where hypoxia is prone to develop, P limitation in the inner estuary and CTZ remains weak owing to the high DIN and DIP levels contributed by the Pearl River. The P limitation intensifies along the plume's path due to the biological uptake of N and P at the Redfield ratio. This substantial P limitation has long been reported to suppress primary production and is suspected to reduce hypoxia in the PRE during summer (Yin et al.,



Fig. 8. Effect of P limitation under different nutrient load and river discharge scenarios. **(A)** Percentage of P-limitation area in the entire plume-impacted region (filled dots) or downstream of the plume-impacted region (blank dots) for different scenarios. The plume-impacted region is defined as having surface salinity under or equaling 33 and the downstream is where surface salinity exceeds 24. The x-axis marks scenarios of different nutrient loads while different colors denote scenarios of different freshwater discharge rates. **(B)** Limitation-induced change in cross-transect oxygen inflow for different scenarios. **(C, D)** Same as (B) but for the change in (C) horizontal advection of oxygen and (D) net local oxygen sink integrated over the coastal transition zone. **(E)** Limitation-induced percentage change in the downstream hypoxic area for different scenarios. The percentage change is computed as (Control - N-only)/N-only \times 100 for each nutrient scenario. **(F)** Same as (E) but for the entire system.

2004, 2011; Yin and Harrison, 2008). Our modeling investigation confirms that P limitation markedly suppresses primary production and hypoxia. However, we show that the weakened hypoxia is not simply a vertical (local) process; that is, the suppressed surface primary production reduces the net subsurface oxygen sink and elevates the bottom oxygen concentration. Instead, the enhanced shoreward oxygen influx due to the elevated downstream bottom oxygen level, which is an external horizontal process, plays an equally important role as the vertical processes in alleviating hypoxia. Furthermore, because the impact of P limitation on hypoxia reverses when P-limitation severity is relatively low, the nutrient management strategy based on impact assessments should not be static but should adapt to changing nutrient limitation conditions when the nutrient reduction strategies take effect.

Our work also suggests that the spatial extent of P limitation, which is relatively easy to measure, can be used as a proxy to predict whether the impact of P limitation amplifies or relieves coastal hypoxia. The spatial extent can guide nutrient management for a specific system. Generally, the more spatially constrained the P limitation is (equivalent to the more rapid transition from P-limited to N-limited condition along the plume's path), the more likely the limitation is to amplify hypoxia. This is because, in a less severe P limitation scenario, the limitationinduced hypoxia reduction upstream would be slight, while the excess N transported downstream would effectively fuel the N-limited water to enhance hypoxia downstream.

Lastly, like all modeling studies, there exist uncertainties in our model simulations. For example, our model does not include the nutrients of a high N/P ratio delivered by submarine groundwater (Dai et al., 2021) that may aggravate P limitation. In addition, the model does not account for the use of organic phosphorus as an alternative P source for phytoplankton growth (Li et al., 2017) or the release of iron-bound P from sediments during hypoxic conditions; both processes may alleviate the P limitation. Future work is needed to understand and quantify the contributions of these different sources and types of phosphorus to the

impact of P limitation on coastal hypoxia. Nonetheless, considering the complexity of the processes involved, the scarcity of observations, and the large uncertainties in model parameterization, focusing on the dominant P source (i.e., riverine DIP) as in our and previous modeling assessments (e.g., Laurent et al., 2014, 2017) is a necessary step to simulating more realistic P dynamics and P-limitation impact on coastal hypoxia.

5. Conclusion

By combining observations with numerical results from a 3D physical-biogeochemical model off the Pearl River Estuary, we illustrate that during the summer upwelling period, the effect of P limitation on coastal hypoxia can reverse from suppression to amplification due to interacting changes in surface primary production and shoreward bottom oxygen influx under high versus low P-limitation severity. We highlight the role of altering shoreward bottom oxygen influx in modulating the effect of P limitation on coastal hypoxia, which has had less historical attention than the downstream-diluted production in P-limitation impact assessments. Finally, we show that the spatial extent of P limitation coastal hypoxia and guide nutrient management in an affected estuarine and coastal system.

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Fig. 9. P-limitation-induced change in the vertical distribution of dissolved oxygen (DO) averaged over the west-east transect for different freshwater discharge scenarios with (A) Baseline N&P, (B) -60%N&P, (C) -70%N&P, and (D) -80%N&P nutrient load, respectively. The shaded area denotes the temporal variation during the neap-spring tidal cycle (Day 38–45).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

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